

## EVOLUTION AND ZOOGEOGRAPHY OF AUSTRALIAN FRESHWATER TURTLES

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The contemporary turtle fauna of Australia comprises freshwater and marine species but no terrestrial taxa. The literature on evolution and zoogeography of the Australian freshwater turtles (Chelidae) is reviewed. Because opposing conclusions were reached in several of these studies, we critically examine each of them. We accept the phylogeny of Georges & Adams (1992); *Elseya* and *Emydura* are not synonymous and *Elseya* consists of the *E. dentata* and *E. latisternum* species groups (generically distinct). However, *Pseudemydura umbrina* shares common ancestry with other Australian short-necked turtles and is their extant sister taxon. The *E. latisternum* group is the sister taxon of the non-*Pseudemydura* Australian short-necked turtle genera.

Understanding pre-Cretaceous dispersal of the ancestral lineage on the South American-Antarctic-Australian supercontinent is important for ascertaining relationships among Australian freshwater turtles. Increasing aridification during the Pleistocene, resulting in isolation within river drainages, appears to have augmented allopatric speciation.

We recognize 23 extant species of Australian chelid turtles in 7 genera: *Chelodina expansa*, *C. longicollis*, *C. novaeguineae*, *C. oblonga*, *C. rugosa*, *C. steindachneri* and one undescribed species; *Elseya dentata* and 3 undescribed species; *Elseya latisternum* and three undescribed species; *Elusor macrurus*; *Emydura macquarrii* (inclusive of *E. australis*, *E. krefftii* and *E. signata*), *E. subglobosa*, *E. victoriae* and 2 undescribed species; *Pseudemydura umbrina*; and *Rheodytes leukops*. Relationships among genera remain enigmatic.

□ Australia, evolution, turtles, zoogeography.

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The reptilian order Testudines contains about 257 living species of turtles (Ernst & Barbour, 1989) in two suborders, Cryptodira and Pleurodira. Cryptodira contains 10 families and about 203 species, and Pleurodira two families and about 54 species. Cryptodiran turtles withdraw the head by vertical flexure of the neck into an S, and the pelvic girdle does not attach to the plastron. Pleurodirans withdraw the head by horizontal flexure of the neck, and the pelvic girdle attaches to the plastron. Each suborder is characterised by its own specialised cervical vertebrae.

Although cryptodirans are more derived than pleurodirans, the former did not stem from the latter (Ernst & Barbour, 1989). The earliest fossils of cryptodiran turtles are Middle Jurassic, 50 million years older than the earliest pleurodiran fossils (Legler & Georges, 1993a). However, the fossil record is poor, and pleurodiran turtles probably originated earlier (Gaffney, 1979; Bull & Legler, 1980; Ernst & Barbour, 1989). The two suborders are probably derived from separate ancestral lineages, each of which presumably could

not withdraw the head because of non-specialised cervical vertebrae (Gaffney, 1977).

Pleurodira contains the Pelomedusidae and Chelidae. Pelomedusids inhabit Africa, Madagascar and South America, but previously also Europe, Asia and North America (Frair, 1980). They retain mesoplastral bones in the shell and a squamosal bone in the skull; thus, Pelomedusidae is plesiomorphic to Chelidae (McDowell, 1983), which lacks mesoplastral and squamosal bones.

The contemporary fauna of Australia comprises freshwater and marine turtles, with a complete absence of terrestrial species. The Australian freshwater turtles are pleurodirans of the Chelidae, with exception of one cryptodiran, *Carettochelys insculpta* of the Carettochelydidae. The latter species inhabits northern Australia and New Guinea, and it is the sole extant member of its family. As recently as the Eocene, Carettochelydidae had a broad distribution in the Northern Hemisphere (Legler & Georges, 1993a). The living marine turtles of Australia are cryptodirans of the Cheloniidae and Dermochelyidae.

TABLE 1. Recent primary research papers that recognize the two nominal turtle genera *Elseya* and *Emydura* as separate, or as congeneric

Separate recognition	Congeneric recognition
Cann & Legler (1994)	Gaffney (1991)
White & Archer (1994)	Gaffney, Archer & White (1989)
Georges (1993)	McDowell (1983)
Georges & Adams (1992)	Gaffney (1981)
Legler (1985)	Frair (1980)
Legler (1981)	Gaffney (1979)
Legler & Cann (1980)	Gaffney (1977)
Burbidge, Kirsch & Main (1974)	

Australia was inhabited also by freshwater cryptodirans of the living Trionychidae (Pliocene - Gaffney & Bartholomai, 1979; Willis, 1993), and possibly Emydidae (middle Miocene; Murray & Megirian, 1992). A primitive non-marine cryptodiran was reported from the Early Cretaceous of Victoria (Gaffney et al., 1992), and also primitive terrestrial turtles that are neither cryptodiran or pleurodiran (Rich & Rich, 1989). Australia was inhabited as recently as the Pleistocene by giant horned terrestrial turtles (shells 1.5m length) of the extinct eucryptodiran Meiolaniidae, which also occurred in South America, Madagascar, Lord Howe Island and New Caledonia (Mittermeier, 1984; Archer et al., 1991). The fossil turtles of Australia were reviewed by Gaffney (1981, 1991) and Molnar (1991).

Outside Australia and New Guinea, the Chelidae inhabit only freshwaters east of the Andes in South America (Iverson, 1992), but a fossil specimen was found in Antarctica (Pritchard & Trebbau, 1984). Although chelids are not the dominant turtle family in South America, they are comparable in diversity to those in Australia. Consequently, constructing a phylogeny of freshwater turtles requires understanding of evolutionary relationships between the two geographically distant groups, together with the Pelomedusidae.

Australian chelids separate into two broad morphological and ecological groups (Goode, 1967; Cann, 1978), long-necked species and short-necked species. *Chelodina* contains long-necked species that spear or ambush their food (Pritchard, 1984; Legler & Georges, 1993b). They have 4 claws on the forelimbs, and a neck at least 2/3 the length of the shell (Cogger, 1992), with which they strike out rapidly and capture prey (Legler, 1993). *Elseya*, *Elusor*, *Emydura*,

*Pseudemydura* and *Rheodytes* are short-necked active foragers (Legler & Georges, 1993b; Cann & Legler, 1994). These have 5 claws on the forelimbs, and a neck less than 1/3 the length of the shell (Cogger, 1992).

South American chelids also separate into long-necked sit-and-wait predators and short-necked active foragers (Ernst & Barbour, 1989). Like Australian long-necked *Chelodina*, South American long-necked *Chelus* and *Hydromedusa* have 4 claws on the forelimbs. Also, like Australian short-necked genera, South American short-necked *Phrynops* and *Platemys* have 5 claws on the forelimbs. The questions are posed: How are the geographically-distant Australian and South American chelids related? Are the similar groups a result of ecological convergence, or do they share common ancestry?

Australian chelids are morphologically conservative (Cogger, 1992), which has hindered the recognition of valid taxa and obscured their true relationships. Discoveries of 3 new genera and 11 new species (Legler & Cann, 1980; Georges & Adams, 1992; Cann & Legler, 1994), of which 1 genus and 9 species await description, have made their phylogeny even more enigmatic. Ecologies of most species are poorly known. There is controversy regarding relationships and validity of taxa, especially the nominal genera and species of *Elseya* and *Emydura* (Table 1). The taxonomy is in a state of flux. Cogger (1992) recognized 15 species in 5 genera; Georges & Adams (1992) recognized 23 species in 7 genera.

This paper has 2 purposes; a review of the literature on evolution and zoogeography of Australian freshwater turtles and a review of opposing published conclusions. We recommend acceptance of one of the proposed phylogenies.

## EVOLUTION OF THE CHELIDAE

The most important evolutionary and zoogeographic studies of Australian freshwater turtles are by Burbidge et al. (1974), Gaffney (1977), Legler & Cann (1980), Legler (1981), McDowell (1983), Georges & Adams (1992), and Cann & Legler (1994). The zoogeographic background was established by Burbidge et al. (1974), McDowell (1983), and Pritchard & Trebbau (1984). The systematic studies by Legler & Cann (1980), Legler (1981), McDowell (1983), and Cann & Legler (1994) approach an ideal sampling strategy. Georges & Adams (1992) sampled extensively and used sensitive bio-

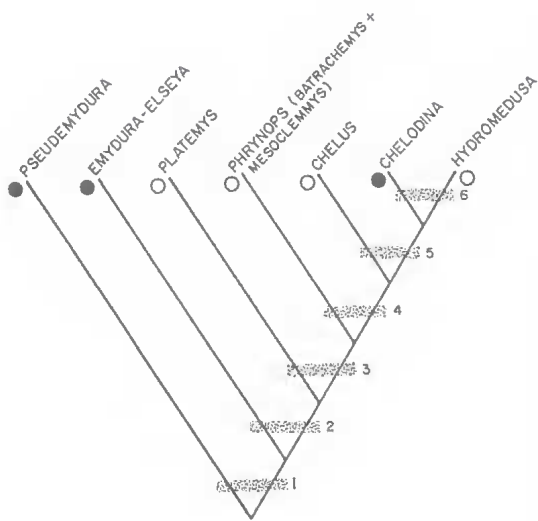


FIG. 1. Relationships within the Chelidae, based upon 26 cranial characters (Gaffney, 1977). Black dots indicate Australian genera, open circles South American genera.

chemical techniques capable of detecting cryptic relationships.

Among the 3 types of systematic methods (evolutionary, phenetic, cladistic), the last has the strongest Popperian scientific basis. Cladistics attempts to test hypotheses by designating characters as either plesiomorphic (ancestral) or derived (descendent). Derived characters shared between taxa are considered evidence of common ancestry unless homoplasy is demonstrated (Hennig, 1966; Brooks & McLennan, 1991). The ingroup is the taxon whose evolutionary relationship is being tested. It is compared to a reference taxon, the outgroup, which is usually considered the sister taxon of the ingroup (Brooks & McLennan, 1991). Determination of the outgroup is a crucial and often most subjective decision in cladistics (Hennig, 1966; Maddison et al., 1984).

Gaffney (1977) undertook a cladistic analysis of living chelids using 26 cranial characters (Fig. 1). On the basis of skull simplification, he designated *Emydura* (inclusive of *Elseya*) as the outgroup of all other chelid genera. By assigning equal weight to all character states, Gaffney (1977) assumed that all changes had equal probability. The Australian long-necked *Chelodina* were shown to be more closely related to South American long-necked *Chellus* and *Hydromedusa* than to Australian short-necked *Emydura* and *Pseudemydura*. The South American short-neck-

ed *Phrynops* and *Platemys* were positioned between *Chelodina* and the Australian short-necked genera.

Although Gaffney (1977) recognized *Elseya* and *Emydura* as congeneric (as did Frair [1980] and McDowell [1983]), this view is not commonly followed (White & Archer, 1994). However, Gaffney et al. (1989) claimed that the two genera are not adequately diagnosed.

*Pseudemydura* shares no derived skull characters with either the Australian and South American long-necked turtles or Australian short-necked turtles, but instead possesses 7 unique skull characters (Gaffney, 1977). Gaffney (1977) erected the monogeneric Pseudemydurinae and considered *Pseudemydura* as sister taxon to other chelids. *Pseudemydura* is autapomorphic among chelids in lacking temporal emarginations of the skull (Gaffney et al., 1989), and *P. umbrina* is unique among turtles by its behavior of excavating the egg chamber with forelimbs rather than hindlimbs (Kuchling, 1993). However, several derived characters are shared between *Pseudemydura* and other Australian short-necked turtles, such as reduced neural bones and cornified head scutes (McDowell, 1983). The intergular scute extending posteriorly to separate the humeral scutes was considered unique and derived in *Pseudemydura* (Burbidge et al., 1974), but McDowell (1983) observed it also in *Elseya dentata* and *Emydura australis*. Thus there may be no need for the Pseudemydurinae.

Because changes in chromosome morphology are quantum changes (King, 1985), cladistic analyses using karyotypes are free from problems associated with measuring continuous variables (King, 1985). Mutations detected by G- and C-banding can be treated as analogues of morphological character states (King, 1985). Evolutionary relationships of the cryptodirans were studied in this manner by Bickham & Baker (1976) and Bickham & Carr (1983). Also using G- and C-banding, Bull & Legler (1980) conducted chromosomal studies of 13 of the 14 pleurodiran genera. However, chelids do not respond well to this staining technique and a cladistic analysis was not done.

Even so, Bull & Legler (1980) gave valuable insight into evolution of chelids. For example, the ancestral karyotype is thought to be the one that most species share (King, 1985). The majority of chelids are uniform in number ( $2n = 50$ ) and bands of their chromosomes, which supports the outgroup designation of *Emydura* (and *Elseya*)





FIG. 2. The position of Australia and Antarctica during the mid Cretaceous (after Rich & Rich [1989]). Black areas in Australia indicate the seaway extant during the Cretaceous.

by Gaffney (1977). The Cryptodira existed during the Early Cretaceous. Because the level of chromosomal variation among cryptodiran families is less than that between the two pleurodiran families, pleurodirans probably originated prior to the Cretaceous (Bull & Lecler, 1980).

McDowell (1983) used osteological and soft organ characters to study relationships of the Chelidae and Pelomedusidae. He concluded that *Elseya* and *Emydura* were the most pelomedusid-like and, thus, plesiomorphic of the Chelidae, which further supported Gaffney's (1977) out-group designation. Specifically, *Elseya dentata* has a longitudinal ridge on the maxilla, a character it shares only with the pelomedusid *Podocnemis* of South America.

Frair (1980) conducted a biochemical study of pleurodirans using total protein electrophoresis and immunoelectrophoresis with phenetic analyses, sampling all Chelidae and Pelomedusidae. He confirmed that each family is monophyletic, as first proposed by Gaffney (1975) and supported the arrangement of Gaffney (1979). Frair (1980) also showed the Chelidae to be more closely related to the Madagascan pelomedusid *Erymnochelys* than to the South American pelomedusid *Podocnemis* and *Peltocephalus*. Thus it appears that the lineage giving rise to the

Chelidae occurred in both South America and Africa when joined 115 million years ago. *Erymnochelys madagascariensis* is a relict species (Pritchard & Trebbau, 1984) and is probably most like the ancestral condition.

Pritchard & Trebbau (1984) reviewed earlier zoogeographic hypotheses of the Chelidae, as well as Pelomedusidae and other living and extinct South American turtles. In light of recent geological and evolutionary studies, along with a fossil chelid from Antarctica of Miocene age, they suggested the Chelidae could have originated in Antarctica. Pritchard & Trebbau (1984) argued that passive dispersal across vast stretches of ocean is possible only for terrestrial turtles. Thus an Antarctic landbridge or narrow sea should be considered in zoogeographic hypotheses of Australian and South American chelids (Fig. 2).

The hypothesis that the Australian long-necked turtles (*Chelodina*) did not originate from Australian short-necked turtles (Gaffney, 1977) is supported by recent biochemical data. Georges & Adams (1992) studied the evolutionary relationships of Australian chelids using allozyme electrophoresis (Hillis, 1987). Their extensive data set included 54 independent loci of 277 specimens of all species (except *Pseudemydura umbrina*) from 76 populations through Australia and New Guinea.

Georges & Adams (1992) employed 3 systematic methods. Their phenetic analysis incorporated principal co-ordinates, which gave representations of genetic distance. The cladistic analysis using PAUP (Swofford, 1985) produced unresolved cladograms because only 14 of 54 loci could be used as characters. A parsimony method (Farris, 1972; Baverstock & Schwaner, 1985) using distance-Wagner and Fitch-Margoliash procedures, which are not widely accepted, also produced unresolved cladograms. Although the several generated phylogenies varied, relationships of some taxa remained constant.

Georges & Adams' (1992) results suggest that divergence between the Australian long- and short-necked turtles is about twice that within either of the two groups; and the level of divergence among the short-necked species is substantially greater than that among the long-necked. These results support Gaffney's (1977) phylogeny in which South American genera are intermediates, and short-necked turtles are probably more primitive.

McDowell (1983) presented a simple dispersal theory to explain Gaffney's (1977) results. The

ancestors of *Emydura* entered South America from Australia. The lineage diverged, giving rise to South American short-necked turtles, from which evolved a long-necked form that dispersed back into Australia.

Neural bones are considered an important taxonomic character for chelids. They were reported absent in all living Australian chelids, except *Chelodina oblonga* (Burbidge et al., 1974; McDowell, 1983). Neural bones were reported in South American chelids, which McDowell (1983) considered evidence for convergence of the long-necked condition. However, Rhodin & Mittermeier (1977) reported low frequencies of neural bones in certain populations of both short- and long-necked Australian chelids.

The Australian long-necked *Chelodina oblonga* and South American chelids possess well-developed neural bones, which in *C. oblonga* vary from 5-8 (Burbidge et al., 1974; Rhodin & Mittermeier, 1977). Neural bones (although reduced in size) persist at low frequencies in certain populations of *Elseya latisternum*, an undescribed *Elseya* sp. from the Manning River (NSW), *C. longicollis*, *C. novaeguineae* and *C. siebenrocki*. Of two fossil specimens of *Emydura* from mid-Tertiary deposits in Tasmania, one has one reduced neural bone and the other none (Warren, 1969a). Apparently the character should be assessed as absent/reduced in size, or well developed (Pritchard, 1984).

The fossil record of chelids is poor, beginning in the Early Cretaceous of Victoria (Warren, 1969b) with a specimen identified first as extant *Emydura macquarrii* but later as *Chelycarapookus arcuatus*. It has well-developed neural bones (Burbidge et al., 1974), and is considered ancestral to short-necked turtles in which neural bones are absent or reduced. Early Cretaceous chelid fossils have been found in NSW and in western QLD (a *Chelycarapookus*-like form; R.E. Molnar, pers. comm.).

*Chelycarapookus arcuatus* was a river-dweller (Molnar, 1991) and probably had a broad distribution in eastern Australia. With vulcanism forming the Great Dividing Range later during the Cretaceous (Galloway & Kemp, 1984), and with increasing aridification during the Pleistocene, the contemporary turtle fauna may have evolved by allopatric speciation.

McDowell's (1983) zoogeographic hypothesis explains certain phylogenetic relationships. The following model is adapted from his, considering that at times Antarctica had a warmer environ-

ment. During the Early Cretaceous, the ancestral lineage including *Chelycarapookus* inhabited the southern supercontinent. During the late Eocene, Australia was isolated by sea, with members of the *Chelycarapookus* lineage left in Australia and in the Antarctic-South American landmass. The trend in neural bones in the Australian lineage was for reduction and loss, giving rise to *Elseya*, *Elusor*, *Emydura*, *Pseudemydura* and *Rheodytes*. The South American lineage retained well-developed neural bones, evolving into the South American short-necked and long-necked turtle genera. However, the ancestral lineage of South American long-necked turtles also dispersed back into Australia, giving rise to Australian long-necked turtles. The general trend for neural bones in this group was for reduction and loss, but well-developed neural bones were retained in the immediate lineage to *Chelodina oblonga*. Morphologically and biochemically, *C. oblonga* is plesiomorphic in its genus (Burbidge et al., 1974; Georges & Adams, 1992).

Why did only the ancestral South American long-necked turtle lineage disperse back to Australia from the Antarctic-South American landmass, and not also the ancestral South American short-necked turtle lineage? The answer might be elucidated by examining ecologies of the two groups. Unlike any South American short-necked turtle genus, in addition to inhabiting freshwaters, the South American long-necked *Hydromedusa* also inhabits estuaries (Ernst & Barbour, 1989). Australian long-necked *Chelodina* (*C. longicollis*, *C. expansa*) has greater resistance to evaporative water loss than Australian short-necked *Emydura* (*E. macquarrii*; Chessman, 1984). *Chelodina* inhabits permanent and temporary freshwaters (Chessman, 1984), and can also tolerate saline waters. During drought, *Chelodina* walks overland and finds other water, or buries into substrate and aestivates (Goode, 1967; Cann, 1978; Grigg et al., 1986). *Chelodina rugosa* can inhabit highly saline ephemeral swamps (Ehmann, 1992), and *C. longicollis* can tolerate brackish water for prolonged periods (Smith, 1993). On the other hand, all Australian and South American short-necked chelids inhabit only permanent freshwaters, except *Pseudemydura* which inhabits ephemeral swamps and aestivates. Thus it appears that the lineage giving rise to Australian long-necked turtles had greater potential for dispersal across land and/or a narrow sea between Australia and the Antarctic-South American landmass.

EVOLUTIONARY RELATIONSHIPS  
AMONG AUSTRALIAN FRESHWATER  
TURTLES

In a study of evolutionary relationships of Australian chelids, the ideal sample would include all species; with specimens from throughout a species' range, of various sizes and both sexes to include the variations of geography, ontogeny and sexual dimorphism. Legler & Cann (1980), Legler (1981), McDowell (1983), Georges & Adams (1992), and Cann & Legler (1994) approach this ideal sampling strategy.

Using cladistic analysis of cranial characters, Gaffney (1977) diagnosed distant chelid genera, but he could not separate *Elseya* from *Emydura*. Because the skull and jaw of chelids are probably correlated conservative characters, the data set appears inadequate for diagnosing closely related genera. In addition, the data were from small samples, often single specimens.

Burbidge et al. (1974) diagnosed *Elseya* from *Emydura* on nuchal and intergular scutes: nuchal scute usually absent in *Elseya*, present in *Emydura*; intergular scute smaller and more rectangular in *Elseya*, larger and less rectangular in *Emydura*. *Elseya* was reported to have an elongate snout. However, data for *Elseya* and *Emydura* were from single specimens of *Elseya latisternum* and *Emydura macquarrii*, their sole representatives of the two genera.

Burbidge et al. (1974) also used phenetics to analyze serological data of Australian chelids. The first 3 dimensions of the principal components described 85% of the variation. Among the short-necked turtles, *Elseya dentata* clustered with *Elseya novaeguineae*; *Emydura australis*, *Emydura krefftii* and *Emydura subglobosa* clustered; and the two groups together formed a closely associated group. *Elseya latisternum*, *Emydura macquarrii* and *Pseudemydura umbrina* were outliers; however, after omitting the anti-*Elseya latisternum* data, *Elseya latisternum* clustered with *Elseya dentata* and *Elseya novaeguineae*. The long-necked turtle species (*Chelodina*) clustered together, but with *C. oblonga* an outlier within the genus.

These results showing *P. umbrina* and *C. oblonga* as outliers to the short-necked and long-necked turtles, respectively, are accepted. Their sera react strongly and they have different morphologies. However, the designation of *Elseya latisternum* as an outlier is treated with caution because its serum reacted weakly.

Bull & Legler (1980) reported the short-necked *Elseya*, *Emydura* and *Rheodytes* to have identical

karyotypes ( $2n=50$  and gross chromosome morphology), and *Pseudemydura* differed only slightly by having chromosome pairs 6 and 10 acrocentric. Pelomedusid turtles differed greatly, with  $2n=26-36$  and 5 large macrosomes.

Using total protein electrophoresis, Frair (1980) observed only one type of electrophoretic pattern among two species of *Elseya* and two *Emydura*. The electrophoregrams of *Elseya latisternum* and *Elseya novaeguineae* were similar, but the former longer and with its cathodal line closer to the negative pole. The electrophoregrams of *Emydura signata* and *Emydura subglobosa* were similar to *Elseya novaeguineae*, but the latter slightly more negative. Among *Chelodina*, there were two electrophoretic patterns: 3 anodal lines for *C. longicollis* and *C. novaeguineae*; and 1 for *C. expansa*, *C. rugosa* and *C. siebenrocki*. Observing little variation between *Elseya* and *Emydura* relative to that within *Chelodina*, Frair (1980) recognized *Elseya* and *Emydura* as synonymous.

Frair (1980) concluded the results of Bull & Legler (1980) (similar chromosome numbers and bands of *Elseya* and *Emydura*) supported their synonymy. However the chromosomes of *Pseudemydura umbrina* and *Rheodytes leukops* are also similar in number and bands to *Elseya* and *Emydura*, but *Pseudemydura* and *Rheodytes* are separate genera because of their unique morphologies.

Frair (1980) also used the observations of Webb (1978) on basking of captive Australian turtles to support synonymy of *Elseya* and *Emydura*: *Elseya* and *Emydura* basked regularly, whereas *Chelodina* never basked. However, basking is prevalent in the South American short-necked chelids *Phrynops* and *Platemys* (Lacher et al., 1986; Monteiro & Diefenbach, 1987); in Pelomedusidae (short-necked turtles) (Miller, 1979); and catholically in the suborder Cryptodira (short-necked turtles), especially the Emydidae (Ernst & Barbour, 1989). Because basking behavior is widespread in short-necked turtles, it has little value in supporting synonymy of *Elseya* and *Emydura*. Rather, it probably indicates ecological differences between short-necked and long-necked turtles.

Legler (1981) examined more than 3000 specimens of Australian chelids and considered geographic distributions to elucidate relationships. He stated that *Elseya dentata* (and at least 3 undescribed species) and *Elseya latisternum* (and at least 1 undescribed species) belonged to separate genera, but no diagnoses were presented.



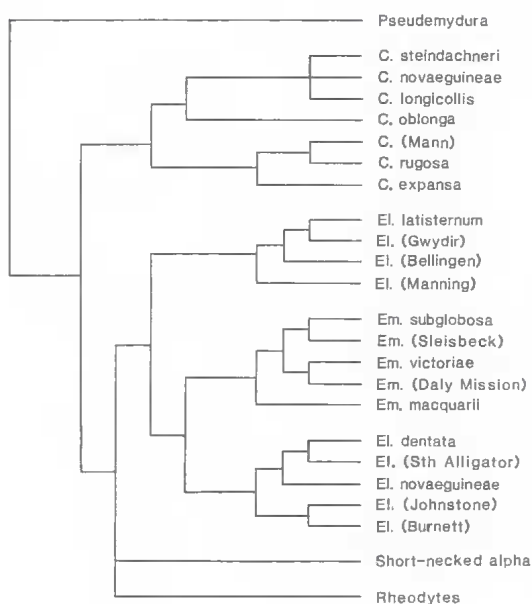


FIG. 3. The phylogeny of Australian freshwater turtles (and *Elseya novaeguineae*), based on allozyme electrophoresis (Georges & Adams, 1992). Short-necked alpha is *Elusor macrurus*.

McDowell (1983) examined at least 5 specimens from various localities of all Australian short-necked turtle species, except *Emydura signata*. Because there were no significant differences among the characters he tested, McDowell (1983) placed *Elseya novaeguineae* in synonymy of *Elseya dentata*; and *Emydura albertisii*, *Emydura krefftii* and *Emydura subglobosa* in synonymy of *Emydura australis*. Also, his results showed *Elseya dentata* (and *Elseya novaeguineae*) to be more closely related to *Emydura australis* than to *Elseya latisternum*, so he recognized *Elseya* and *Emydura* as synonyms. However, the biochemical results of Georges & Adams (1992) argue against these synonymies. In addition, there are pronounced color differences among the nominal species of *Emydura*. In life *Emydura subglobosa*, commonly called the painted turtle, has a crimson plastron and yellow on the face (Legler, 1981). Living *Emydura* sp. (Daly, Nicholson and Roper Rivers) has red on the face and legs, and *Emydura krefftii* yellow across the head (Cann, 1978; Cogger, 1992). But the significance of color pattern in diagnosing short-necked turtles remains unknown.

On allozyme characters, Georges & Adams (1992) could not distinguish between *Emydura*

*macquarii*, *E. krefftii* (including Cooper Creek and Fraser Island populations) and *E. signata*, all of which they considered to be *E. macquarii*. Georges (1993) regarded *E. macquarii* as polytypic or a species complex, with unresolved systematic positions of distinctive populations in Cooper Creek and Fraser Island and the taxa referred to as *E. krefftii* and *E. signata*.

Although *Elseya latisternum* was an outlier to other *Elseya* species (and *Emydura*), neither Burridge et al. (1974) nor Frair (1980) suggested that *Elseya* was paraphyletic. In serological studies like Frair's (1980), the variation of electrophoregrams is misconstrued by multiple protein analysis (Baverstock & Schwaner, 1985). However, monovalent techniques with antisera for single proteins are more amenable to genetic interpretation because the strength of cross reaction is directly proportional to differences in the gene locus encoding the protein (Baverstock & Schwaner, 1985). Georges & Adams (1992) considered single locus protein variation and consequently has the same objectivity as monovalent immunological methods.

Georges & Adams' (1992) principal co-ordinates analysis of the first 3 dimensions described 63% of the variation. Australian chelids clustered into 5 groups, which were recognised by Legler (1981). *Elseya novaeguineae*, which McDowell (1983) placed in synonymy of *Elseya dentata*, had a divergence level similar to that of *Elusor* and *Rheodytes* to the *Elseya dentata* group. This species also lost its affinities with the *Elseya dentata* group in higher dimensions.

The highest levels of divergence were within *Elseya* and *Chelodina*; that within *Emydura* was relatively small, suggesting its 5 species are relatively young. Divergence between *Elseya* and *Emydura* was less than that within *Elseya*. The *Elseya dentata* group was closer to *Emydura* than to the *Elseya latisternum* group, which was established also by McDowell (1983). However, instead of recognizing *Elseya* and *Emydura* as congeneric, Georges & Adams (1992) considered the *Elseya latisternum* group to comprise a separate genus, their rationale that synonymization would have to include also *Elusor* and *Rheodytes*. The genetic distances between the provisional genera (*Elseya dentata* group, *Elseya latisternum* group, *Emydura*) are similar to, if not greater than, that between many of the cryptodiran emydid genera, especially the batagurines (Sites et al., 1984).

In regard to Australian long-necked *Chelodina*, the phylogenetic results of Georges & Adams

TABLE 2. Distribution of Australian freshwater turtles (Georges & Adams 1992) and *Elseya novaeguineae*. From Cogger (1992), Ehmann (1992), Georges & Adams (1992), Iverson (1992), Legler & Georges (1993b), Georges (1993). ?=systematic position of the population is unresolved. Zoogeographic regions from Fig. 4

GROUP	SOUTH-WESTERN	WESTERN	CENTRAL	SOUTHEASTERN		EASTERN	NORTHERN		NEW GUINEA
				WESTERN	EASTERN		WESTERN	EASTERN	
<i>Chelodina expansa</i>				<i>expansa</i>		<i>expansa</i>	<i>rugosa</i>		
							sp. (Liverpool + Mann R.)		
<i>Chelodina longicollis</i>		<i>steindachneri</i>		<i>longicollis</i>				<i>longicollis</i>	
							<i>novaeguineae</i>		
<i>Chelodina oblonga</i>	<i>oblonga</i>								
<i>Elseya dentata</i>						sp. (Burnett + Fitzroy R.)	sp. (South Alligator R.)	sp. (Johnstone R.)	<i>novaeguineae</i>
							<i>dentata</i>		
<i>Elseya latisternum</i>				sp. (Gwydir R.)	<i>latisternum</i>				
					sp. (Bellingen R.)				
					sp. (Manning R.)				
<i>Elusor</i>						<i>macrurus</i>			
<i>Emydura</i>			? (Cooper C. + Diamantina R.)	<i>macquarrii</i>		<i>krefflii</i> ?	<i>victoriae</i>	<i>krefflii</i> ?	
						<i>signata</i> ?		<i>subglobosa</i>	
						? (Fraser I.)	sp. (Daly, Mitchell + South Alligator R.)		
							sp. (Daly, Nicholson + Roper R.)		
<i>Pseudemydura</i>	<i>umbrina</i>								
<i>Rheodytes</i>						<i>leukops</i>			

(1992) aligned with the species groups established by their principal components analysis. In general, their interpretation of relationships agreed with Burbidge et al. (1974) and Legler (1981); however, contrary to Legler (1981), the level of divergence between the *C. expansa* and *C. longicollis* groups did not warrant separate generic recognition.

Georges & Adams (1992) tentatively placed *Elusor* and *Rheodytes* outside the *Elseya dentata*, *Elseya latisternum* and *Emydura* radiation (Fig. 3). Although the cladograms of Georges & Adams (1992) were unresolved, their phenetic analysis suggests both *Elusor* and *Rheodytes* have their closest affinities with the *Elseya dentata* group. Similarly, the PAUP-generated cladogram of Cann & Legler (1994), based upon 35 morphological and 16 allozyme characters treated equally and compared to *Chelodina* as the outgroup, suggests *Elusor* and *Rheodytes* form the sister group to the *Elseya dentata* group.

Cann & Legler (1994) also performed multidiscriminate analyses with 31 mensural charac-

ters from large samples (n=41-1000) of the *Elseya dentata* group, *Elseya latisternum* group, *Elusor*, *Emydura* and *Rheodytes*. The data were treated as percentages of carapace length. In the resulting 3D scatter plots, the groups separated equidistant from each other but with *Emydura* separate from all. Consequently, Cann & Legler (1994) recognized the *Elseya dentata* group, *Elseya latisternum* group, *Elusor* and *Rheodytes* as the *Elseya* group of genera.

The primary weakness of Cann & Legler's (1994) multidiscriminate analysis is that a species' morphology is adaptive to its environment. For example, extrapolation from Cann & Legler (1994) would suggest that Australian short-necked chelids are more closely related to short-necked emydid turtles than to Australian long-necked chelids. Also, sample groups must be of similar sex and age classes to negate sexual and ontogenetic differences in morphology. For example, 90% of Cann & Legler's (1994) sample of *Elusor macrurus* were small juveniles. If this species experiences ontogenetic changes in mor-



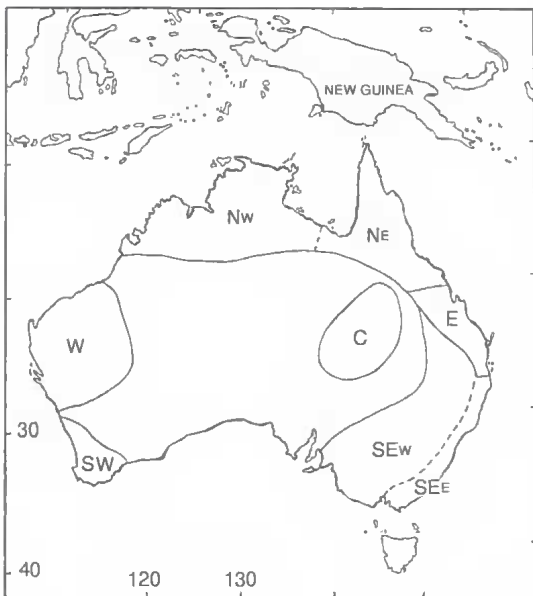


FIG. 4. The zoogeographic regions of Australian freshwater turtles (modified from Burbidge et al., 1974). Species within each region are listed in Table 2.

phology, then comparison against a sample of another species except of similar composition is meaningless.

The relationship of *Pseudemydura umbrina* to other Australian chelids remains obscure. Its endangered status and small population size (Kuchling & DeJose 1989) limit certain avenues of research (e.g. Georges & Adams 1992). Nonetheless, *P. umbrina* shares several derived characters with other Australian short-necked turtles, but none with South American genera or Australian long-necked *Chelodina* (McDowell, 1983). Thus *Pseudemydura* may be the sister taxon to other Australian short-necked turtles.

#### REPRODUCTIVE PATTERNS OF AUSTRALIAN FRESHWATER TURTLES

Examining the ecology of a species can help elucidate its evolutionary history: knowing functions of structures makes the grading of character states more accurate, and it gives insight into selective pressures for higher or lower rates of speciation (Shine, 1985). Legler (1985) recognized 2 patterns of reproduction among Australian chelids, one having evolved in the tropics and the other in temperate environments.

The two reproductive patterns were defined by egg size and hardness, time of nesting and length

of incubation (Legler, 1985). The tropical strategy invoked large hard eggs being deposited during the dry season (winter) with long incubation; and the temperate strategy, smaller flexible eggs deposited in spring or summer with relatively short incubation.

A temperate origin was indicated (Legler, 1985) for the *Elseya latisternum* group (*E. latisternum* and at least 3 undescribed species), *Chelodina longicollis* group (*C. longicollis*, *C. novaeguineae*, *C. steindachneri*) and *Emydura*. A tropical origin was indicated for the *Elseya dentata* group (*E. dentata*, *E. novaeguineae* and two undescribed species) and *C. expansa* group (*C. expansa*, *C. oblonga*, *C. rugosa*).

However, the two patterns are not realistic and the criterion for egg hardness was only subjectively defined. For example, the *C. expansa* and *E. dentata* groups lay the largest eggs (Legler, 1985), but these species are the largest Australian freshwater turtles. Also, larger eggs may necessarily be harder because of structural constraints. In cryptodirans there is positive correlation between adult size and egg size; egg size and hatching size; and for hard shelled eggs, egg size and shell thickness (Ewert, 1979). Also, some tropical species lay soft shelled eggs, and some both hard and soft (Moll & Legler, 1971; Ewert, 1979).

Legler (1985) was selective of data from previous authors, ignoring that which lessened distinction between the two patterns. For example, *C. oblonga* (proposed tropical origin) nests during summer (Burbidge, 1967, 1984) and *C. expansa* (proposed tropical origin) sometimes during autumn (Goode & Russell, 1968; Georges, 1984); and eggs of *C. longicollis* (proposed temperate origin) undergo long incubation, up to 200 days (Cann, 1978). Thus it appears that additional reproductive patterns exist. Also, if the contrasting tropical and temperate environments are strong selective pressures on reproduction, why do some species of each group inhabit the other environment? Within *Emydura* (proposed temperate origin), *E. subglobosa*, *E. victoriae* and 2 undescribed species inhabit only the tropics; and *E. macquarrii* (inclusive of *E. australis*, *E. krefftii* and *E. signata*) inhabits both temperate and tropical environments (Cogger, 1992; Iverson, 1992). Georges et al. (1993) previously questioned the fit of Legler's (1985) reproductive patterns to species groups.

However, according to the centre of diversity rule (Ross, 1974), *Emydura* probably evolved in the tropics, and also the *Elseya dentata*, *C. expansa* (*C. expansa*, *C. rugosa* and an undescribed

species in the NT, sensu Georges & Adams [1992]) and *C. longicollis* groups. With 3 species in the temperate zone and *Elseya latisternum* inhabiting both temperate and tropical zones, the *E. latisternum* group probably evolved in temperate environments. In addition, the groups for which the centre of diversity rule predicts tropical origins all have representatives and/or closely related species in New Guinea, dispersal northward having been possible by Pleistocene landbridges (Burbidge et al., 1974). On the other hand, the *Elseya latisternum* group (predicted temperate origin), with *E. latisternum* ranging from northern NSW (temperate) to the tip of Cape York Peninsula, has no close relative in New Guinea.

#### ZOOGEOGRAPHY OF AUSTRALIAN FRESHWATER TURTLES

Zoogeographic regions for Australian freshwater turtles were defined by Burbidge et al. (1974), which in general corresponded to those for freshwater fish (Whitley, 1959). However, we also recognize Central and Eastern zoogeographic regions for freshwater turtles (Fig. 4, Table 2). The Central Region is in the arid zone of interior Australia and contains the Cooper Creek and Diamantina River population of large macrocephalous *Emydura*, which Ehmann (1992) and Legler & Georges (1993b) reported to be an undescribed species. Although Georges & Adams (1992) could not distinguish the population by allozyme electrophoresis from *E. macquarrii*, Georges (1993) regarded it as a distinctive population with unresolved systematic position. The Eastern Region encompasses the Fitzroy, Burnett, Mary and Brisbane river drainages, to which are endemic only an undescribed species of the *Elseya dentata* group (Georges & Adams, 1992), *Elusor macrurus* and *Rheodytes leukops*. Our Central and Eastern regions correspond to Whitley's (1959) Sturtian and Krefitian regions, respectively. Zoogeographic regions for freshwater turtles are almost identical to those for freshwater fish. Also, like some freshwater fish, some freshwater turtles inhabit both northern Australia and southern New Guinea.

The vicariance hypothesis of Burbidge et al. (1974) suggests that ancestors of each species group were distributed widely throughout northern and eastern Australia during the Pleistocene epoch when the climate was cooler and wetter. The existing chelid fauna resulted by allopatric

speciation, directed by isolation of river drainages with increasing aridification.

Southwestern Australia is inhabited by endemic *Chelodina oblonga* and *Pseudemydura umbrina*. This region became isolated by formation of a broad inland sea from the Gulf of Carpentaria to the coast of S AUST during the Early Cretaceous (Rich & Rich, 1989; Fig. 2). Burbidge et al. (1974) proposed that the eastern *Chelodina* ancestor evolved into the form lacking neural bones, and the eastern *Pseudemydura* became extinct. Prior to the Cretaceous sea, *Elseya* and *Emydura* had tropical northern distributions. Later during the Cretaceous the sea receded, leaving a vast waterless desert equally impenetrable. Alternatively, Pritchard & Trebbau (1984) suggested two separate invasions from Antarctica, one each into eastern and western Australia.

The distributions of freshwater turtle and fish species groups support the vicariance hypothesis of Burbidge et al. (1974). The species within each group are largely allopatric, with sympatry between species of different groups (Legler, 1981; Iverson, 1992). In addition, there are fossils and a relict population of *Emydura* in the arid zone of SW QLD and adjacent S AUST (Gaffney, 1979; Ehmann, 1992); and fossils of *Pseudemydura* (early to middle Miocene) from Riversleigh, on the Gulf of Carpentaria (Gaffney et al., 1989).

Burbidge et al. (1974) showed *C. oblonga* to be morphologically and serologically an outlier to other *Chelodina*. Similarly, the phenetic analysis (3D) of Georges & Adams (1992) showed *C. oblonga* to be an outlier within the *C. expansa* group (although this was not maintained at higher dimensions), and their phylogenetic analyses consistently placed *C. oblonga* as pleisiomorphic. These results together with retention of well-developed neural bones (Burbidge et al., 1974) indicate that *C. oblonga* approaches the ancestral condition, further supporting Burbidge's et al. (1974) vicariance hypothesis.

The hypothesis of Burbidge et al. (1974) requires the short-necked turtle genera to have a northern distribution prior to formation of the inland Cretaceous sea. However, the *Elseya latisternum* group probably had a southeastern origin, and thus potential for dispersal into southwestern Australia. The following hypotheses may explain the absence of the *Elseya latisternum* group from southwestern Australia. (1) The *E. latisternum* lineage previously inhabited also southwestern Australia but has since become extinct there. (2) The southern Australian environment during the Cretaceous was not favorable for

dispersal of the *E. latisternum* lineage westward into southwestern Australia. (3) The *E. latisternum* lineage evolved after the Cretaceous, and since then the southern Australian environment has not been favorable for dispersal westward.

Hypotheses (2) and (3) appear most likely because members of the *E. latisternum* group live in the headwaters of rivers, even above major waterfalls in the Great Dividing Range of eastern Australia (Legler, 1981). Low flat land, instead of elevated ranges, between SE and SW Australia may have been a barrier to dispersal of this group. On the other hand, if *Emydura* had a temperate distribution prior to formation of the inland Cretaceous sea, the genus could have dispersed westward into southwestern Australia.

*Rheodytes leukops* Legler & Cann (1980) and *Elusor macrurus* Cann & Legler (1994) belong to monotypic genera and with highly restricted ranges. *Rheodytes leukops* is endemic to headwaters of the Fitzroy River, E of the Great Dividing Range in central eastern Queensland. The species is highly specialised for inhabiting rapids: it feeds on invertebrates in rapids, and it can obtain all of its oxygen through its enlarged cloacal bursae (Legler & Georges, 1993b). The other short-necked turtles feed in slow-moving or standing water (Legler & Georges, 1993b), and their cloacal bursae are less developed. *Elusor macrurus* is endemic to the Mary River drainage of SE QLD, also E of the Great Dividing Range, and its biology is poorly known (Cann & Legler, 1994)

#### CONCLUDING STATEMENT

Although we now have a better understanding of Australian chelids, 1 genus and 9 extant species await description (Georges & Adams, 1992), and the systematic positions of several populations of *Emydura* remain unresolved: Cooper Creek, Fraser Island, and the taxa referred to as *E. krefftii* and *E. signata*. Intergeneric relationships remain enigmatic. However, it appears that *Pseudemydura umbrina* shares common ancestry with other Australian short-necked turtles and is their sister taxon. Also, it appears the *Elseya latisternum* group is the sister taxon of the non-*Pseudemydura* short-necked turtles, as suggested by data from Georges & Adams (1992) and Cann & Legler (1994).

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